



Implicit reward associations impact face processing: Time-resolved evidence from event-related brain potentials and pupil dilations



Wiebke Hammerschmidt^{a,b}, Igor Kagan^{a,c}, Louisa Kulke^{a,b}, Annekathrin Schacht^{a,b,*}

^a Leibniz ScienceCampus "Primate Cognition", Kellnerweg 4, Göttingen 37077, Germany

^b Affective Neuroscience and Psychophysiology Laboratory, Institute of Psychology, University of Göttingen, Göttingerstraße 14, Göttingen 37073, Germany

^c Decision and Awareness Group, Cognitive Neuroscience Laboratory, German Primate Center/Leibniz Institute for Primate Research, Kellnerweg 4, Göttingen 37077, Germany

ARTICLE INFO

Keywords:

Event-related brain potentials (ERPs)
Implicit associative learning
Motivational context
Motivational salience
Pupil dilations

ABSTRACT

The present study aimed at investigating whether associated motivational salience causes preferential processing of inherently neutral faces similar to emotional expressions by means of event-related brain potentials (ERPs) and changes of the pupil size. To this aim, neutral faces were implicitly associated with monetary outcome, while participants ($N = 44$) performed a face-matching task with masked primes that ensured performance around chance level and thus an equal proportion of gain, loss, and zero outcomes. During learning, motivational context strongly impacted the processing of the fixation, prime and mask stimuli prior to the target face, indicated by enhanced amplitudes of subsequent ERP components and increased pupil size. In a separate test session, previously associated faces as well as novel faces with emotional expressions were presented within the same task but without motivational context and performance feedback. Most importantly, previously gain-associated faces amplified the LPC, although the individually contingent face-outcome assignments were not made explicit during the learning session. Emotional expressions impacted the N170 and EPN components. Modulations of the pupil size were absent in both motivationally-associated and emotional conditions. Our findings demonstrate that neural representations of neutral stimuli can acquire increased salience via implicit learning, with an advantage for gain over loss associations.

To support adaptive behavior in complex environments, the human brain developed efficient selection mechanisms that bias perception in favor of salient information. In order to address the variety of different sources of salience, conventional attention theories focusing on goal- and salience-driven attention mechanisms (Corbetta and Shulman, 2002; Connor et al., 2004) were extended by the assumption of a fundamental value-driven attention mechanism (Anderson, 2013; for a recent review, see Failing and Theeuwes, 2017). This mechanism is discernible not only in stimuli inherently carrying salience, but also in stimuli associated with motivational valence, all sharing similar attentional prioritization. In line with this account, not only physical stimulus features but also emotional and motivational factors have been demonstrated to determine increased salience of certain stimuli and directly impact attention and visual processing capacities (e.g., Zeelenberg et al., 2006), resulting in a facilitated sensory encoding at initial processing stages (e.g., Della Libera and Chelazzi, 2006). Stimuli of particularly high inherent salience are faces,

for which involuntarily capture of attention and preferential processing has been documented, presumably due to their crucial role in human social interactions. This face-superiority effect has been reliably demonstrated on a behavioral level in object recognition/perception tasks (e.g., Langton et al., 2008), and moreover in studies employing visual search tasks or attentional blink paradigms including facial expressions of emotions (Eastwood et al., 2001; Anderson, 2005; for a review, see Vuilleumier, 2005; Calvo and Lundqvist, 2008). Particularly, facial expressions of emotions convey various types of relevant information in social interactions (for a review, see Frith, 2009) and are regarded as evolutionarily prepared stimuli (e.g., Öhman and Mineka, 2001). Faces with and without emotional expressions are thus ideal stimuli in experiments investigating effects of inherent versus associated salience as they allow for a direct comparison of these effects within an overall relevant stimulus domain.

Due to their high temporal resolution, event-related brain potentials

* Corresponding author. Affective Neuroscience and Psychophysiology Laboratory, Institute of Psychology, University of Göttingen, Göttingerstraße 14, Göttingen 37073, Germany.

E-mail address: aschach@uni-goettingen.de (A. Schacht).

<https://doi.org/10.1016/j.neuroimage.2018.06.055>

Received 31 December 2017; Received in revised form 8 June 2018; Accepted 19 June 2018

Available online 22 June 2018

1053-8119/© 2018 Elsevier Inc. All rights reserved.

(ERPs) allow segregating different processing stages and therefore gaining insights to the mechanism underlying the face-superiority effect as well as the processing advantage of facial expressions of emotions over time. Attentional priority for facial expressions of emotion and their sustained preferential processing over neutral faces is reflected in several dissociable ERP components (e.g., Schupp et al., 2004; Rellecke et al., 2012). Especially two ERP components have been linked to subsequent stages of emotion processing in humans: the EPN and the LPC. The Early Posterior Negativity (EPN), a relative negativity over posterior electrode sites, typically starting around 150–200 ms after stimulus onset (e.g., Junghöfer et al., 2001; Rellecke et al., 2011), has been suggested to reflect enhanced sensory encoding of facial expressions of emotion. The EPN is typically followed by the Late Positive Complex (LPC) or Late Positive Potential (LPP, e.g., Cuthbert et al., 2000; Schupp et al., 2004) over centro-parietal electrodes, starting around 300 ms after stimulus onset (e.g., Rellecke et al., 2011). This long-lasting ERP response has been assumed to reflect higher-order elaborate and evaluative processes (for a review, see Olofsson et al., 2008; Schacht and Sommer, 2009; Rellecke et al., 2011). In addition, two earlier components were recently found to be modulated by emotional expressions. First, the P1 component, peaking around 100 ms after stimulus onset, consists of bilateral occipital positivities and reflects the activation of extrastriate visual areas via selective attention (Di Russo et al., 2003). Some studies reported enhanced P1 amplitudes for emotional facial expressions in comparison to neutral facial expressions (e.g., Batty and Taylor, 2003; Rellecke et al., 2011), indicating that emotional salience impacts early perceptual encoding. Second, the N170, consisting in a negativity over temporo-occipital electrodes, has been functionally linked to holistic face perception (e.g., Bentin et al., 1996) and has been shown to be modulated by emotional expressions (for reviews, see Rellecke et al., 2013; Hinojosa et al., 2015).

Previous studies have demonstrated that even inherently neutral faces can gain salience through associated emotional context information, reflected in augmented EPN (e.g., Suess et al., 2013; Wieser et al., 2014) and LPC amplitudes (Klein et al., 2015; Xu et al., 2016). Also modulations of the early P1 component were demonstrated (Abdel Rahman and Sommer, 2012) elicited by faces associated with biographical knowledge. However, in particular motivational salience might arise from a variety of other sources, driven by an explicit motivational context or by acquired associations. Contexts might determine motivational dispositions – e.g., the readiness to act in given situations – as they can confront a person with appealing opportunities and daunting obstacles (Scheuthle et al., 2005) and thus directly influence behavior. An increase of the motivational salience of a given context can be generated by introducing reinforcements as incentives (Meadows et al., 2016). In a recent ERP study, Wei and colleagues (Wei et al., 2016) showed that the expectation of monetary gain – indicated by motivationally relevant cues – impacted the processing of negative and neutral target words over consecutive stages from sensory encoding (EPN) to higher-order evaluation (P3/LPC). Interestingly, motivational incentives have been recently demonstrated to affect the processing of abstract target symbols even before effects of spatial attention (Bayer et al., 2017). In addition, a “cue-P3” component directly elicited after cue onset with enhanced amplitudes for reward-indicating as compared to loss-indicating cues was reported (Zheng et al., 2017).

Driven by the compelling evidence for impacts of motivational contexts and inherent emotional valence, the question arises under which conditions salience can be acquired. A fruitful approach to test this assumption is provided by associative learning paradigms that allow investigating the influences of acquired salience without interference with stimulus-driven salience. Aiming at a direct comparison between inherent and associated saliences, Hammerschmidt and colleagues (Hammerschmidt et al., 2017) reported that explicit reward-associations to inherently neutral faces elicited increased P1 responses during delayed testing. The elicitation of typical emotion-related ERP components at longer latencies (EPN and LPC), was, however, restricted to facial

expressions of emotion. In contrast, employing a highly similar learning paradigm as in the study by Hammerschmidt et al. (2017), Rossi and colleagues (Rossi et al., 2017) detected an increase of the P3 to reward-associated unknown single letters from unfamiliar alphabets. Importantly, the processing advantage reported for stimuli associated with motivational salience is not restricted to rewards but has also been demonstrated for associations with aversive events, gratings associated with negative affective pictures (Stolarova et al., 2006), auditory shocks (Hintze et al., 2014) or unknown single letters associated with monetary loss (Rossi et al., 2017), mainly present on the perceptual level.

ERPs reflect processing differences on the neural level whereas physiological arousal – one of the key components of emotions (Scherer 2005, 2009; Lang and Bradley, 2010) – is reflected amongst other indicators in changes of the pupil size, which have been related to norepinephrine release in the locus coeruleus (Berridge and Waterhouse, 2003; Einhäuser et al., 2008; Gilzenrat et al., 2010; Laeng et al., 2012; Murphy et al., 2014). Therefore, pupil activity can be used as a measure of attentional, cognitive and emotional processing (Smallwood et al., 2011; Kang et al., 2014), with increased pupil size in response to emotionally arousing pictures (Bradley et al., 2008) and auditory stimuli (Partala and Surakka, 2003). In particular, inherently angry faces paired with an angry body induced larger pupil dilations than fearful and happy face-body pairs (Kret et al., 2013). Moreover, motivational modulations through outcome associations, in addition to stimuli of inherent emotional salience, can also increase pupil size, demonstrated for both reward (e.g., Massar et al., 2016) and loss incentives (Pulcu and Browning, 2017). Interestingly, modulations of pupil dilation further depend on task difficulty, manipulated through mental effort (Mathôt et al., 2015; Peysakhovich et al., 2015), and decision uncertainty (Kahneman, 1973; Satterthwaite et al., 2007; Brunyé and Gardony, 2017; Urai et al., 2017), with greater pupil dilations occurring with increasing task difficulty. The parallel measurement of ERPs, pupil dilations and behavioral data might help to elucidate the multiple components involved in emotion processing (e.g., Grandjean et al., 2008).

In line with Anderson's assumption (Anderson, 2013) of a value-driven attention mechanism, previous research, including our previous study (Hammerschmidt et al., 2017), clearly indicated that both emotional and motivational aspects have a direct impact on visual stimulus processing. Nevertheless, the specific conditions, under which learning mechanisms or different contexts can modify a certain stimulus' salience, are not fully understood, presumably contributing to heterogeneous findings in the past. Despite the great progress in this area of research, there are a number of open questions that we aimed to address in the present study: Firstly, effects of associated motivational salience occurred during several processing stages mainly in explicit associative learning paradigms (e.g., Stolarova et al., 2006; Schacht et al., 2012; Hintze et al., 2014; Hammerschmidt et al., 2017; Rossi et al., 2017). However, it seems reasonable that inherent, motivation- or emotion-based salience might have been acquired implicitly, that is without explicit knowledge about the hedonic value of the certain stimulus. Hence, one of the yet unresolved questions is whether implicit and explicit associations of motivational salience have similar effects on stimulus processing. Implicit learning is generally linked to participants' problems with an explicit recall (Berry and Dienes, 1993), often characterized as a ‘complex form of priming’ (Cleeremans et al., 1998). Further, it was argued that implicit representations possibly need more time and cognitive resources to be generated than information learned explicitly (Batterink and Neville, 2011). Recently, it could be demonstrated that reward associations have a direct impact on spatial attention – even when presented implicitly (Bourgeois et al., 2016). The authors implicitly associated target symbols with a reward cue and could show that reaction times were slower when a previously reward-associated symbol was presented together with distractors indicating that reward associations might be learned without awareness. Using the Stroop task, Krebs and colleagues (Krebs et al., 2010) could show that task-irrelevant stimuli might gain salience through implicit

reward associations. Secondly, it remained open whether the impacts of associated gain and loss might be symmetric under conditions of equalized outcomes, as successful learning usually implies an increase of gain in parallel to reduced losses (e.g., Hammerschmidt et al., 2017; Rossi et al., 2017).

The main aim of the current study was to investigate potential effects of implicitly learned associations of motivational salience to inherently neutral facial stimuli in direct comparison to effects elicited by inherent facial expressions of emotion. Therefore, we employed a prime-face matching task with masked prime presentation, implementing performance at chance level and thus an equalization of performance-dependent gain, loss, or zero-outcome conditions. During the learning session, colored cues were presented at the beginning of each trial, indicating the motivational condition which was kept constant for each of the target faces. During the test session, the same task was employed, however, without any performance-dependent monetary incentives or outcome. In addition to the previously associated faces, facial expressions of emotion of novel identities were presented, allowing for a comparison of effects driven by associated motivational and inherent emotional salience, similar to the design of our previous study (Hammerschmidt et al., 2017). In addition, we collected ERP and pupil size data during the learning and test sessions with the aim to test the impact of motivational contexts on subsequent stimulus processing (cf., Wei et al., 2016) and to allow the investigation of the temporal characteristics and autonomous physiological correlates of association-related effects on the following day. We expected that the cue-indicated reward or loss context would boost sensory processing of task-relevant face stimuli in the visual cortex (Bayer et al., 2017), resulting in enhanced P1 amplitudes after target face onset. Aiming at expanding the findings by Zheng and colleagues (Zheng et al., 2017) that showed augmented P3 amplitudes elicited by reward-indicating visual cues, we further tested potential modulations of cue-evoked ERPs by different motivational contexts. As the incentive values of the cue stimuli were made explicit to our participants, these simple symbolic stimuli might carry increased salience similar to stimuli with emotional/motivational content and thus trigger increased amplitudes of EPN and LPC components. Pupil dilations should be increased in condition of high motivational salience (Massar et al., 2016; Pulcu and Browning, 2017). Based on the findings from our previous study (Hammerschmidt et al., 2017), we expected increased amplitudes of early ERP components, i.e., the P1, for inherently neutral faces previously associated with monetary gain. Loss-associations might trigger similar effects as gain-associations (especially on the N170 component; Hammerschmidt et al., 2017) as both incentive conditions were equalized – in terms of frequency of occurrence and amount of monetary outcome – during the learning session. Faces with happy and particularly with angry expressions should elicit larger P1, N170, EPN and LPC amplitudes than neutral expressions (e.g., Schupp et al., 2004; Schacht and Sommer, 2009; Rellecke et al., 2011; Hammerschmidt et al., 2017). For pupil dilations during the test session, we expected an increase for angry compared to happy and neutral expressions (Kret et al., 2013).

Materials and methods

Participants

Data was collected from fifty-five participants. Seven participants were excluded due to EEG artifacts in either the learning or test session, and four due to strategies that successfully countered visual masking during the face-matching task (the performance exclusion criterion was defined as an individual performance-dependent bonus exceeding average bonus $\pm 2SDs$ across participants in the learning session). The remaining forty-four participants (21 female) were ranging in age between 18 and 32 years (mean age = 24.0 years, $SD = 3.5$), with normal or corrected-to-normal vision and without neurological or psychiatric disorders according to self-report. Forty-two participants were right-handed (according to Oldfield, 1971). Participants received 8 euro per hour or

course credit; in addition, the individual monetary bonus achieved during the learning session was disbursed.

Stimuli

Facial stimuli were selected from the Karolinska Directed Emotional Faces (KDEF) database (Lundqvist et al., 1998). An ellipsoid mask surrounded all facial stimuli within an area of 130×200 pixels (4.59×7.06 cm, $4.6 \times 7.1^\circ$) in order to eliminate hair, ears and clothing, and to leave only the face area visible.

For the learning session, twelve colored pictures of faces (6 female, 6 male) with inherently neutral expressions were used as target faces. The same pictures served as primes in matching trials; additional twelve pictures of inherently neutral faces (6 female, 6 male) were used as nonmatching primes. Hence, 24 different face stimuli in total were used in the learning session. Diamond-shaped cues of 120×120 pixels (3.18×3.18 cm) indicated the outcome category (reward, loss, zero outcome) of the given trial in three different equiluminant colors (blue, pink, and brown). Grey circles were used as feedback stimuli (248×248 pixels, 5×5 cm) indicating the amount of monetary outcome won or lost in the preceding trial in the corresponding cue color.

During the test session, the same twelve prime-target combinations of the previously associated faces were presented as in the learning session the day before. In addition to these faces, twelve novel identities (6 female, 6 male) showing emotional (joy, anger) and neutral expressions (in total $N = 36$ face stimuli) were presented both as target faces and matching primes. Importantly, the expressions of the 12 target face identities (4 for happy, neutral, and angry, respectively) were counterbalanced across participants. Another twelve new identities (6 female, 6 male) showing facial expressions of emotion (joy, anger) or neutral expressions, ($N = 36$ face stimuli) were used as prime stimuli in non-matching trials. Thus, 96 different face stimuli in total were used in the test session ($24 + 36 + 36$). Target and prime faces always matched with respect to gender and emotional expressions. For each face stimulus of both learning and test session (in total $N = 96$), a scrambled version was generated and used as mask for the preceding primes. All facial stimuli were matched offline for luminance (according to Adobe Photoshop CS6™), $F(23,72) = 0.873$, $p = 0.631$. All stimuli were presented in the center of the screen on a light grey background.

Procedure

The study was conducted in accordance with the Declaration of Helsinki and approved by the local ethics committee of the Institute of Psychology at the University of Göttingen. Participants were informed about the procedure of the study and gave written informed consent prior to both sessions of the experiment. The study consisted of a learning (~60 min) and a test session (~90 min), which were completed on two subsequent days. The experiment was performed using Presentation® software (Version 18.0, Neurobehavioral Systems, Inc., Berkeley, CA, www.neurobs.com). Participants were seated in a dimly lit, sound-attenuated room, in front of a computer screen (refresh rate 100 Hz; controlled via a photodiode) at a distance of 57 cm. Participants placed their chin and forehead on a head rest in order to avoid movements and ensure correct recording of pupil sizes. After pupil diameter calibration, participants received detailed instructions about the experimental task.

In the learning session, twelve inherently neutral faces were implicitly associated with monetary gain, loss, or zero outcome via an associative learning paradigm. At the beginning of each trial, a diamond-shaped cue indicated the monetary outcome context condition (gain, loss, or zero outcome: no gain/loss). The assignment of the cue's color was fixed for each participant but counterbalanced across participants. The meaning of the cues and the feedback scheme was explained prior to the experiment, but the fixed associations between each face and its motivational context were not made explicit. Participants were asked to decide whether the identity of the presented target face was matching the

preceding prime face – irrespective of the presented cue. In the gain condition, the correct classification of the face-matching task was awarded with +50 cents (incorrect classifications = 0 cents). A correct classification in the loss condition prevented the participants from the loss of money (0 cents), whereas an incorrect classification led to a loss of 50 cents. For the zero-outcome condition, feedback was either +0 cents (correct classification) or –0 cents (incorrect classification). Responses were given by a button press; correct/incorrect-buttons as well as prime-target assignments were counterbalanced, but consistent within one participant. In the face-matching task, prime and target faces differed in 50% of the trials in identity but were always matched with respect to gender. In case the participant missed to answer a trial within 5000 ms, 70 cents were removed from the bonus. Stimuli were presented block-wise with a total of 20 blocks. Each block consisted of the 12 target faces presented twice in randomized order, paired with a matching (50%) or a non-matching (50%) prime, resulting in 480 trials in total. Importantly, the cue-target face associations (4 target faces per motivational condition) remained stable during the learning session for each participant but were counterbalanced in order to exclude any potential effects of physical stimulus features on the ERP components of interest. At the beginning of each trial (see Fig. 1), a fixation cross was presented in the center of the screen for 1000 ms, followed by the diamond-shaped cue, which was visible for 500 ms. Subsequently, a fixation cross was shown for 200 ms followed by the prime face for 10 ms. The mask appeared for 200 ms followed by a fixation cross for 200 ms. The target face was shown up to 5000 ms, disappearing with button press. The feedback was displayed for 1000 ms. Blocks were separated by a break of self-determined duration, in which the current amount of the individual bonus was displayed. Participants started with a base pay of 10 euro and achieved an individual monetary bonus according to their performance ranging between –11 and 18 euro (*mean* = 1.11 euro, *SD* = 5.98 euro); participants finishing the learning session with a negative balance received the full base payment of 10 euro.

In order to check whether the associations of the presented cue and the target face remained implicit, a manipulation check was implemented at the end of the learning session. The twelve target face identities were presented simultaneously, randomly arranged on the computer screen. The participants were asked to explicitly assign them to

one of the three outcome contexts (gain/zero outcome/loss). This task was repeated about 30 minutes later.

The test session took place on the following day, to allow for memory consolidation. The face-matching task remained the same, however, no cue or corresponding feedback was provided, and participants could not win or lose any money (see Fig. 1). The test session consisted of ten blocks with previously associated faces and another ten blocks with novel identities showing emotional (happy, angry) or neutral expressions. The former blocks consisted of the twelve target faces, which were implicitly associated with monetary outcome context the day before. The latter blocks consisted of twelve novel identities with neutral and emotional facial expressions (4 for happy, neutral, and angry, respectively) serving as target faces and primes in matching trials, and twelve additional novel identities with neutral and emotional expressions (4 for happy, neutral, and angry, respectively) serving as primes in the non-matching trials. Each target face was presented twice with a matching and twice with a non-matching prime in randomized order (*N* = 48 trials per block). Each block was repeated ten times (all presented in randomized order), resulting in 20 blocks and 960 trials in total per face condition. The blocks were separated by breaks of self-determined duration. Again, a manipulation check was conducted at the end of the test session to control whether participants paid attention to the target faces: the 24 target face identities of the experiment including the target faces of the learning session (*N* = 12) and the additional novel identities shown only in the test session (*N* = 12) were presented on the computer screen in random order all expressing neutrality. The participants were asked to indicate for each face whether it has been already presented during the learning session the day before, or not. Fig. 2 gives an overview of the study's procedure both for the learning and the test session.

Acquisition and pre-processing of ERP and pupil data

The EEG was recorded from 64 electrodes, placed in an electrode cap (Easy-Cap, Biosemi, Amsterdam, Netherlands) according to the international 10–20 system (Pivik et al., 1993). The common mode sense (CMS) electrode and the driven right leg (DRL) passive electrodes were used as reference and ground electrodes (<http://www.biosemi.com/faq/cms&drl.htm>). Six external electrodes were used: Two on the left and

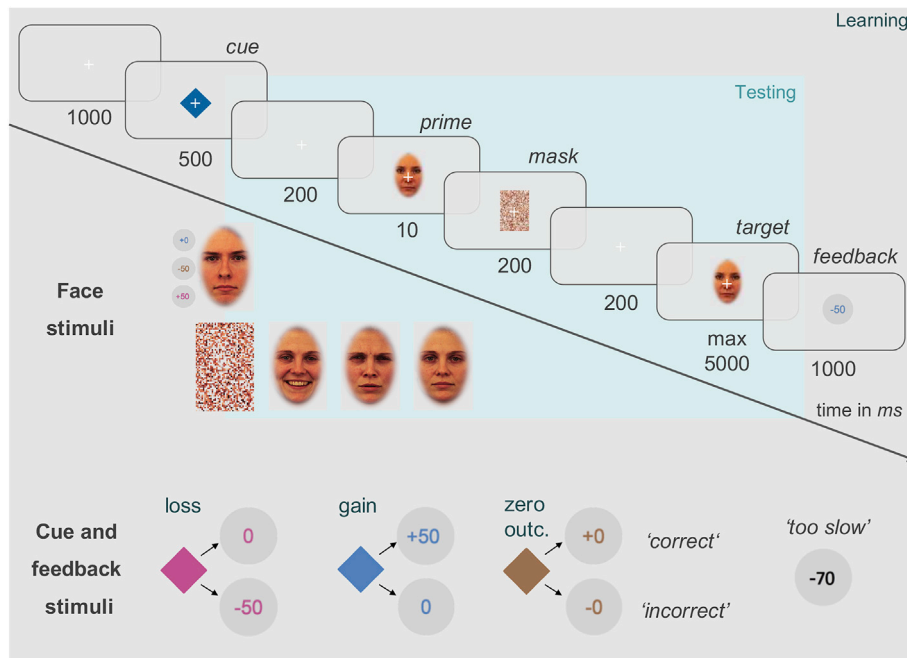


Fig. 1. Trial schemes of the learning and test (blue background, without motivational cue and feedback presentation) sessions with detailed time sequence of the face-matching task.

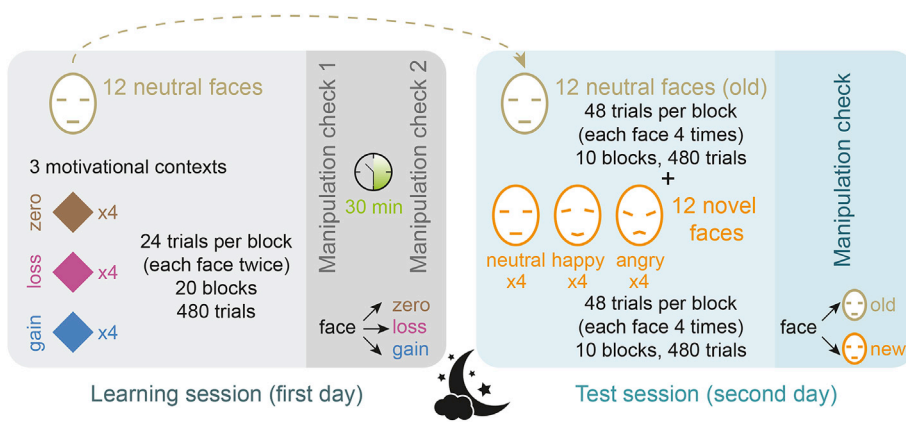


Fig. 2. Procedure of the learning and test session. The learning session included only inherently neutral target faces ($N = 12$); each face was consistently preceded by one of three motivational contexts (for each subject, 4 faces were associated with zero outcome, 4 with potential loss and 4 with potential gain, signified by $\times 4$ for each context). In the test session, in addition to these previously seen 12 faces ('old'), 12 novel faces, 4 with neutral, 4 with happy and 4 with angry expressions, served as targets in separate blocks.

right mastoids respectively, and four external electrodes were placed on the outer canthi and below the eyes to record eye movements and blinks. Signals were recorded at a sampling rate of 512 Hz and a bandwidth of 102.4 Hz (http://www.biosemi.com/faq/adjust_filter.htm), offline filtered with a Low Cutoff (0.03183099 Hz, Time constant 5 s, 12 dB/oct), a High Cutoff (40 Hz, 48 dB/oct) and a Notch Filter (50 Hz). Data was processed using BrainVision Analyzer (Brain Products GmbH, Munich, Germany). Data was down-sampled to 500 Hz (via spline interpolation), average-referenced and corrected for ocular artifacts (blinks) using Surrogate Multiple Source Eye Correction with default parameters (MSEC; Ille et al., 2002) as implemented in BESA (Brain Electric Source Analysis, MEGIS Software GmbH, Gräfelfing, Germany). Application of Surrogate MSEC is detailed in Scherg (2003). The continuous EEG signal of the learning session was segmented into epochs of 2310 ms, starting 200 ms before cue onset and referred to a 200 ms pre-cue baseline. The continuous EEG signal of the test session was segmented into epochs of 1610 ms, starting 200 ms before prime onset and referred to a 200 ms pre-prime baseline. Based on previous research (Hammerschmidt et al., 2017), time windows and regions of interest (ROIs) electrodes for ERP components were chosen as follows for the learning session (related to cue onset): P1 cue: 75–125 ms; EPN cue: 200–300 ms; LPC cue: 350–500 ms; P1 fixation cross1: 585–635 ms; P1 prime/mask: 760–810 ms; P2 prime/mask: 885–935 ms; P1 fixation cross2: 985–1035 ms; P1 target: 1185–1235 ms; N170 target: 1240–1290 ms; EPN target: 1310–1460 ms; LPC target: 1460–1810 ms. For the test session (related to target face onset): P1: 75–125 ms, N170: 130–180 ms, EPN: 200–350 ms, P3: 200–350 ms, LPC: 350–700 ms. ERPs were quantified as most positive (P1, P2) or negative (N170) peak using a semi-automatic peak detection (P1 at O1 and O2, reference electrode: O2; N170 at P9 and P10, reference electrode: P10; P2, O1 and O2, reference electrode: O2) or mean amplitudes (EPN at P9, P10, Iz, Oz, O1, O2, PO7, and PO8; LPC at Pz, P1, P2, CPz, and POz).

Pupil diameter was recorded binocularly using a desktop-mounted eyetracker (EyeLink 1000, SR Research) at a 500 Hz sampling rate. Prior to the experiment, pupil diameter was calibrated with an artificial pupil placed on the lid of the left eye of the participants to set the baseline for the measurement of the pupil dilation size. Offline, analyses of pupil diameter were performed using Matlab. Trigger codes of pupil and EEG data were synchronized.

Pupil data from two subjects were excluded due to technical failure of the eye tracker in the learning or test session, respectively. For each participant and the learning and test sessions separately, artifacts were identified as samples in which the difference in pupil size to the subsequent sample was higher than 0.1 mm or the difference in pupil size from the median across the session was higher than 1 mm. Artifacts were interpolated using a linear interpolation based on the clean data samples. Eleven subjects had to be excluded after artifact correction due to excessive artifacts that could not be interpolated in either the learning or

the test session. One additional subject was excluded because the measured pupil size exceeded the average across subjects by more than 10 SDs. The remaining pupil size data was segmented into epochs from 200 ms prior to cue (learning session)/prime (test session) onset to 7000 ms after. For each subject and condition, pupil size time courses were averaged across both eyes and correct and incorrect responses and corrected to a baseline 200 ms before cue (learning session)/prime (test session) onset. Mean pupil size between 1500 and 4000 ms after cue/prime onset (based on the response latency after cue onset measured by Bayer et al., 2017) was computed for each subject and condition.

Data analyses

All parameters – reaction times (RTs), accuracy (in percent), ERP peaks or mean amplitudes, and pupil diameter – were analyzed with repeated-measures (rm) ANOVAs, separately for the learning session and test session. Outliers were identified as reaction times (RTs) below 200 ms or exceeding $+2SDs$ from the mean per condition and were excluded from behavioral data analysis. RmANOVAs on data from the learning session included the factor Motivation (gain, zero outcome, and loss). Data from the test session were analyzed in separate rmANOVAs, including the factor Motivation (gain, zero outcome, and loss) for learned faces or the factor Emotion (happy, neutral, and angry) for novel faces with emotional expressions. Accuracy deviations from chance level, across the sample and on the individual subject level, were analyzed using the exact test for equality of several binomial proportions to a specified standard (Krishnamoorthy et al., 2004; Unakafov, 2017).

For topography comparisons, the mean ERP amplitudes of all 64 electrodes were divided by global field power (GFP; Skrandies, 1990) per condition to extinguish amplitude differences. Differences of the particular conditions were measured and compared with the topography of another ERP component via rmANOVAs with the factor Electrode (64) and the factor Topography (2).

All post-hoc pairwise comparisons were Bonferroni-corrected.

Results

Effects of motivational context in the learning session

Behavioral data

Descriptive values for behavioral performance measures of the learning session are provided in Table 1. Accuracy on the face-matching task during the learning session was at 50% chance level (not different from the expected random binomial distribution with 0.5 probability, $p > 0.05$, Bonferroni-corrected), and was not impacted by the factor Motivation, $F(2,86) = 0.149$, $p = 0.850$, $\eta_p^2 = 0.003$. Additional analysis of accuracy per target face is reported in Supplementary Materials (Fig. S1). Mean reactions times (RTs) of the learning session significantly

Table 1

Mean reaction times in ms, accuracy in face-matching task and manipulation check in %, during/after face-matching task in the learning session (*SEMs* in parentheses), contrasted for factor levels of Motivation. For the manipulation checks, participants had to assign each of 12 faces to one of the three motivational contexts, but they were not aware that each context has been associated to 4 faces and were not given any feedback during or after the check. The chance level for the manipulation checks was 33%.

Learning Session	Face-Matching Task		Manipulation Checks	
	RTs	Accuracy	1st Check	2nd Check
	Gain	1019 (49)	51 (0.7)	57 (3.3)
Zero	960 (44)	51 (0.6)	48 (4.6)	48 (3.9)
Loss	1079 (51)	51 (0.7)	45 (3.4)	47 (3.7)

differed as a function of the factor Motivation, $F(2,86) = 24.929, p < 0.001, \eta^2_p = 0.367$, with increasing RTs from zero-outcome to gain-, $F(1,43) = 11.206, p = 0.006, \eta^2_p = 0.207$, and loss-context, $F(1,43) = 32.284, p < 0.001, \eta^2_p = 0.429$, and from gain- to loss-context trials, $F(1,43) = 35.894, p < 0.001, \eta^2_p = 0.455$.

Correct assignments of the target faces to motivation conditions – obtained directly after the learning session (1st check) and after 30 min delay (2nd check) – were above 33% chance level for gain- and zero-outcome-associated faces ($p < 0.05$, Bonferroni-corrected, the exact test for equality of several binomial proportions to a specified standard), but did not reach significance for loss-associated faces, without any performance improvement after 30 min delay, $F(1,43) = 0.006, p = 0.940, \eta^2_p = 0.000$.

Table 2

Repeated-measures ANOVA results for all ERP and pupil size data (time windows are referring to cue onset) of the learning session, including F-, p- and η^2_p -values. Only significant post-hoc pairwise comparisons are reported. All post-hoc pair-wise comparisons were Bonferroni-corrected.

Learning Session	Main Effect Motivation	Gain—Zero Outcome	Loss—Zero Outcome	Gain—Loss
P1 Cue (75–125 ms)	$F(2,86) = 0.477$ $p = 0.608$ $\eta^2_p = 0.011$			
EPN Cue (200–300 ms)	$F(2,86) = 7.960$ $p = 0.001$ $\eta^2_p = 0.156$	$F(1,43) = 10.295$ $p = 0.009$ $\eta^2_p = 0.193$	$F(1,43) = 14.837$ $p < 0.001$ $\eta^2_p = 0.257$	
LPC Cue (350–500 ms)	$F(2,86) = 37.755$ $p < 0.001$ $\eta^2_p = 0.468$	$F(1,43) = 52.145$ $p < 0.001$ $\eta^2_p = 0.548$	$F(1,43) = 26.100$ $p < 0.001$ $\eta^2_p = 0.378$	$F(1,43) = 22.067$ $p < 0.001$ $\eta^2_p = 0.339$
P1 fixation cross1 (585–635 ms)	$F(2,86) = 8.752$ $p = 0.001$ $\eta^2_p = 0.169$	$F(1,43) = 16.513$ $p < 0.001$ $\eta^2_p = 0.277$	$F(1,43) = 7.115$ $p = 0.033$ $\eta^2_p = 0.142$	
P1 prime/mask (760–810 ms)	$F(2,86) = 13.959$ $p < 0.001$ $\eta^2_p = 0.245$	$F(1,43) = 25.947$ $p < 0.001$ $\eta^2_p = 0.376$	$F(1,43) = 10.699$ $p = 0.006$ $\eta^2_p = 0.199$	
P2 prime/mask (885–935 ms)	$F(2,86) = 5.934$ $p = 0.005$ $\eta^2_p = 0.121$		$F(1,43) = 10.981$ $p = 0.006$ $\eta^2_p = 0.203$	
P1 fixation cross2 (985–1035 ms)	$F(2,86) = 1.500$ $p = 0.229$ $\eta^2_p = 0.034$			
P1 target (1185–1235 ms)	$F(2,86) = 1.731$ $p = 0.184$ $\eta^2_p = 0.039$			
N170 target (1240–1290 ms)	$F(2,86) = 0.866$ $p = 0.424$ $\eta^2_p = 0.020$			
EPN target (1310–1460 ms)	$F(2,86) = 1.081$ $p = 0.344$ $\eta^2_p = 0.025$			
LPC target (1460–1810 ms)	$F(2,86) = 0.508$ $p = 0.592$ $\eta^2_p = 0.012$			
Pupil size (1500–4000 ms)	$F(2,58) = 32.871$ $p < 0.001$ $\eta^2_p = 0.531$	$F(1,29) = 43.413$ $p < 0.001$ $\eta^2_p = 0.600$	$F(1,29) = 33.466$ $p < 0.001$ $\eta^2_p = 0.536$	

ERP data

Results for all ERP and pupil size data of the learning session are summarized in **Table 2**.

ERPs elicited by motivational cues. EPN mean amplitudes between 200 and 300 ms after cue onset differed as a function of Motivation, $F(2,86) = 7.960, p = 0.001, \eta^2_p = 0.156$, for gain- compared to zero-outcome-, $F(1,43) = 10.295, p = 0.009, \eta^2_p = 0.193$, and loss- compared to zero-outcome-related trials, $F(1,43) = 14.837, p < 0.001, \eta^2_p = 0.257$. LPC mean amplitudes between 350 and 500 ms after cue onset were also modulated by Motivation, $F(2,86) = 37.755, p < 0.001, \eta^2_p = 0.468$, with enhanced amplitudes for gain- compared to zero-outcome-, $F(1,43) = 52.145, p < 0.001, \eta^2_p = 0.548$, for loss- compared to zero-outcome-, $F(1,43) = 26.100, p < 0.001, \eta^2_p = 0.378$, and for gain-compared to loss-related trials, $F(1,43) = 22.067, p < 0.001, \eta^2_p = 0.339$. The P1 elicited by motivational cues was not impacted by the factor Motivation, $F(2,86) = 0.477, p = 0.608, \eta^2_p = 0.011$ (see **Fig. 3**).

As can be seen in **Fig. 3**, the impacts of motivational context were long-lasting. Therefore, ERPs between cue and target face presentation were analyzed to investigate potential impacts of motivational context. The P1 component following the first fixation cross after cue presentation was modulated by the Factor Motivation, $F(2,86) = 8.752, p = 0.001, \eta^2_p = 0.169$, with enlarged peak amplitudes for reward- compared to zero-outcome-, $F(1,43) = 16.513, p < 0.001, \eta^2_p = 0.277$, and loss-compared to zero-outcome-related context, $F(1,43) = 7.115, p = 0.033, \eta^2_p = 0.142$. Motivational context further influenced the P1 component following prime/mask, $F(2,86) = 13.959, p < 0.001, \eta^2_p = 0.245$, with larger positivities for reward- compared to zero-outcome-, $F(1,43) = 25.947, p < 0.001, \eta^2_p = 0.376$, and loss- compared to zero-outcome-related context, $F(1,43) = 10.699, p = 0.006, \eta^2_p = 0.199$. The

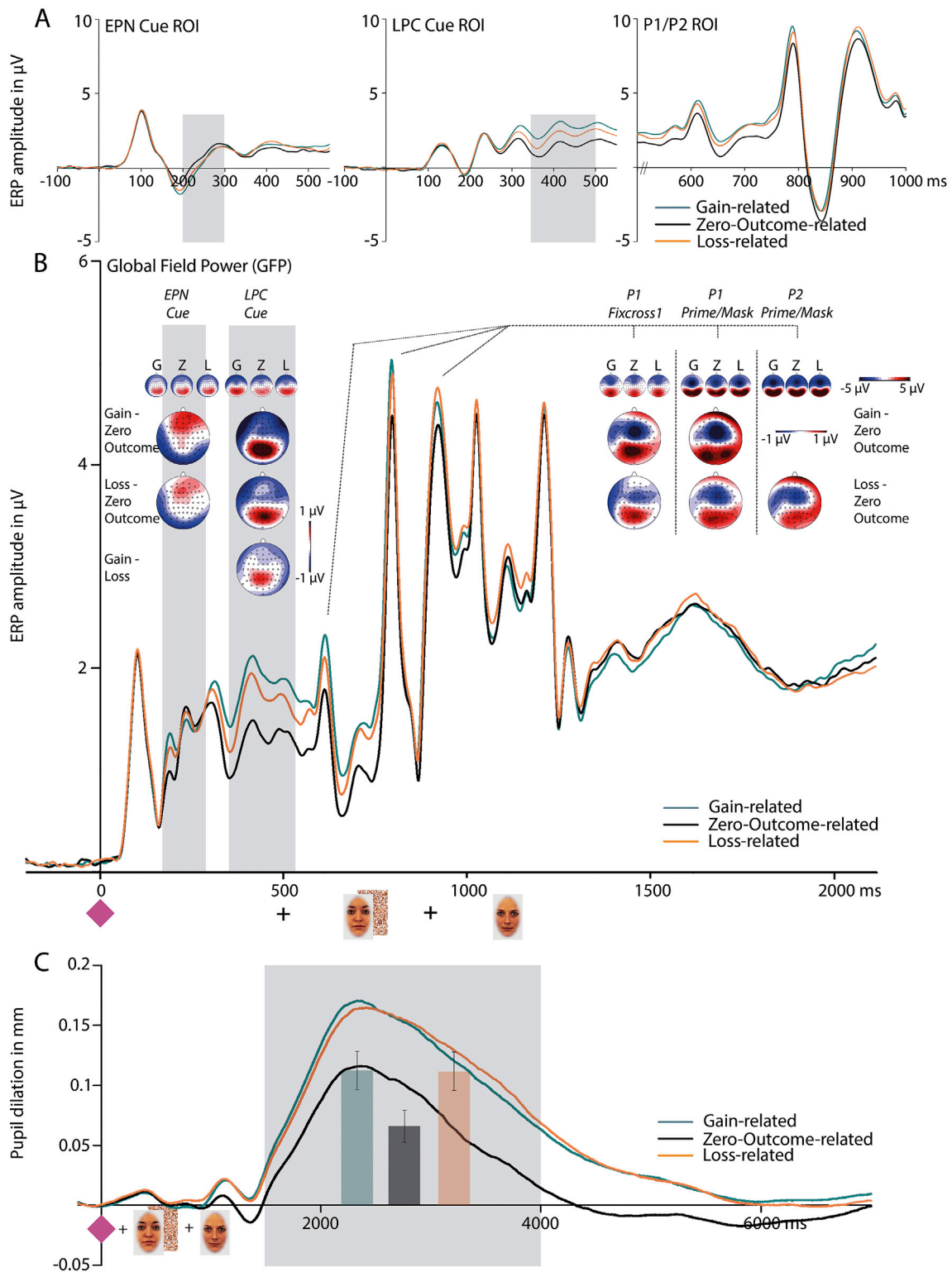


Fig. 3. ERP effects of the learning session for Cue-EPN and Cue-LPC for associated faces and the following peaks. **A:** Regions of interest (ROIs) for the corresponding analyses. **B:** GFP waveform of a complete trial for gain-, zero-outcome- and loss-related faces including ERP topography of raw distributions (small topographies) and differences between indicated motivation categories. Highlighted areas display the time windows of Cue-ERP analyses, P1/P2 peaks of the after-cue/pre-target face interval were analyzed with peak detection in the following time windows: P1 fixation cross1 585–635 ms; P1 prime/mask: 760–810 ms; P2 prime/mask: 885–935 ms after cue onset. **C:** Pupil dilation responses to gain-, zero-outcome-, and loss-related contexts, the highlighted area displays the time window of pupil dilation analysis with means and SEMs embedded as bar chart.

visual P2 following prime/mask was also modulated by the Factor Motivation, $F(2,86) = 5.934, p = 0.005, \eta^2_p = 0.121$, with enhanced peak amplitudes for loss- compared to zero-outcome-related context, $F(1,43) = 10.981, p = 0.006, \eta^2_p = 0.203$. The fixation cross response following the prime/mask was not modulated by the factor Motivation anymore, $F(2,86) = 1.500, p = 0.229, \eta^2_p = 0.034$ (see Fig. 3, panels A and B).

ERPs to target faces. According to rmANOVAs, modulations of peak amplitudes for P1, $F(2,86) = 1.731, p = 0.184, \eta^2_p = 0.039$, and N170 components, $F(2,86) = 0.866, p = 0.424, \eta^2_p = 0.020$, and mean amplitudes for EPN, $F(2,86) = 1.081, p = 0.344, \eta^2_p = 0.025$, and LPC components, $F(2,86) = 0.508, p = 0.592, \eta^2_p = 0.012$, by implicitly associated motivational salience were absent.

Pupil dilations. For pupil dilation data of the learning session, an rmANOVAs showed a significant within-subjects effect of Motivation, $F(2,58) = 32.871, p < 0.001, \eta^2_p = 0.531$, with increased pupil diameters for gain- compared to zero-outcome-, $F(1,29) = 43.413, p < 0.001, \eta^2_p = 0.600$, and loss- compared to zero-outcome-related trials, $F(1,29) = 33.466, p < 0.001, \eta^2_p = 0.536$ (see Fig. 3, panel C).

Effects of associated motivational and inherent emotional salience in the test session

Behavioral data

Descriptive values for behavioral performance measures of the test session are provided in Table 3. In contrast to the learning session, the accuracy on the face-matching task in the test session across the sample of 44 subjects was slightly above the 50% chance level ($M_s = 51\text{--}53\%$, $p < 0.05$, Bonferroni-corrected). In particular, five subjects showed a significant accuracy above (4 subjects, accuracy 58–65%) or below chance level (one subject, 40%) across all three motivational conditions, for the previously associated faces ($p < 0.05$). Similarly, six subjects (four same as for the motivational conditions) showed above chance accuracy for novel faces across all three emotional conditions (58–70%). Accuracy was not impacted by the factors Motivation/Emotion, $F(2,86) = 0.114, p = 0.892, \eta^2_p = 0.003$, and did not differ between conditions (learned faces/novel faces), $F(1,43) = 1.371, p = 0.248, \eta^2_p = 0.031$. During the test session, RTs were not modulated by the Factors Motivation/Emotion, $F(2,86) = 0.183, p = 0.833, \eta^2_p = 0.004$, and Condition, $F(1,43) = 3.045, p = 0.088, \eta^2_p = 0.066$.

After the test session, all 24 target face identities (all showing neutral expressions) from both learning and test session were presented to the participants (2 subjects did not complete the retrieval). Participants had to assign those identities to either the previously seen target faces from the day before or to the novel target faces of the test session (average performance: $M = 84.0\%$, $SEM = 2.5\%$), to control for familiarization with the target faces. The factor Motivation (gain-, loss-, or zero-outcome-related context in the learning session) did not impact accuracy of identifying previously seen target faces, $F(2,82) = 1.563, p = 0.216, \eta^2_p = 0.037$. For novel target faces which were presented with

emotional expressions during the test session, a main effect of the factor Emotion (happy, angry, or neutral expression) was detected, $F(2,82) = 4.173, p = 0.020, \eta^2_p = 0.092$, with higher accuracy rates for angry compared to neutral expressions, $F(1,41) = 7.280, p = 0.030, \eta^2_p = 0.151$.

ERP data

Results for all ERP and pupil size data of the test session are summarized in Table 4.

ERP effects of associated motivational salience. RmANOVAs on ERPs revealed a significant main effect of the factor Motivation on LPC mean amplitudes for faces associated with motivational salience, $F(2,86) = 10.632, p < 0.001, \eta^2_p = 0.198$, with increased amplitudes for gain- compared to zero-outcome-associated faces, $F(1,43) = 18.792, p < 0.001, \eta^2_p = 0.304$, and to loss-associated faces, $F(1,43) = 8.880, p = 0.015, \eta^2_p = 0.171$ (see Fig. 4, panel C and D). P1, $F(2,86) = 0.893, p = 0.413, \eta^2_p = 0.020$, N170, $F(2,86) = 1.241, p = 0.293, \eta^2_p = 0.028$, and EPN amplitudes, $F(2,86) = 1.547, p = 0.219, \eta^2_p = 0.035$, to associated faces were not influenced by the factor Motivation, when tested in the a-priori defined time windows and ROIs. To underline the assumption of implicit learning, we additionally excluded the target faces correctly assigned in the second manipulation check of the learning session and recalculated the analysis in the LPC time window. Again, a significant main effect for the factor Motivation was revealed, $F(2,72) = 5.280, p = 0.007, \eta^2_p = 0.128$, with enhanced amplitudes for gain- compared to zero-outcome-associated faces, $F(1,37) = 10.911, p = 0.006, \eta^2_p = 0.228$.

Further ERP effects of associated motivational salience prior to the LPC component. The time window 200–350 ms after target face onset, in which no EPN modulation for associated motivational salience occurred, was visually re-inspected (see Fig. 4, panel D). ERP distributions and corresponding topographies bore a high resemblance to the LPC effect (350–700 ms) of associated motivational salience outlined above. This impression was confirmed by a topography comparison on normalized ERPs, $F(63,2709) = 1.690, p = 0.077, \eta^2_p = 0.038$. Therefore, ERP activity in this time window was reanalyzed applying the centro-parietal LPC ROI which revealed significant effects of associated motivational salience, $F(2,86) = 5.124, p = 0.008, \eta^2_p = 0.106$, with enhanced amplitudes for gain- compared to zero-outcome-associated faces, $F(1,43) = 8.346, p = 0.018, \eta^2_p = 0.163$.

ERP effects to facial expressions of emotion in novel identities. N170 peak amplitudes to the target faces were significantly impacted by the factor Emotion, $F(2,86) = 7.901, p = 0.001, \eta^2_p = 0.155$, with enhanced negativities for angry compared to neutral, $F(1,43) = 13.695, p = 0.003, \eta^2_p = 0.242$, and happy expressions, $F(1,43) = 8.941, p = 0.015, \eta^2_p = 0.172$. EPN mean amplitudes of novel emotional expressions were significantly modulated by the Factor Emotion, $F(2,86) = 21.217, p < 0.001, \eta^2_p = 0.330$, with enhanced amplitudes for happy compared to neutral, $F(1,43) = 34.587, p < 0.001, \eta^2_p = 0.446$, and for angry compared to neutral facial expressions, $F(1,43) = 39.982, p < 0.001, \eta^2_p = 0.482$. P1 peak and LPC mean amplitudes for novel faces with emotional expressions were unaffected by the Factor Emotion, $F(2,86) = 1.790, p = 0.173, \eta^2_p = 0.040$, and $F(2,86) = 1.266, p = 0.287, \eta^2_p = 0.029$ (see Fig. 4, panel A, B and C).

Pupil dilations. An rmANOVA showed no significant within-subjects effect of associated motivational salience on pupil size, $F(2,58) = 0.049, p = 0.950, \eta^2_p = 0.002$. Pupil size in response to novel facial stimuli with emotional expressions did not significantly differ, according to an rmANOVA, $F(2,58) = 0.705, p = 0.498, \eta^2_p = 0.024$ (see Fig. 5).

Additional topography comparisons. As there is only little previous evidence (cue-P3; Zheng et al., 2017) for emotion/motivation-related ERP modulations following a motivational cue, it remains an exploratory question whether a P3 modulation or an EPN modulation could be evoked prior to P3/LPC modulations, driven by the valence of the cue. To support the results of visual inspection indicating that the ERP difference modulations between 200 and 300 ms after cue onset resemble an

Table 3

Mean reaction times in ms, accuracy in task and familiarity manipulation check in %, during/after face-matching task in the test session ($SEMs$ in parentheses), contrasted for all factor levels of Motivation/Emotion. The chance level for the manipulation check was 50%.

	Face Matching Task		Manipulation Check
	RTs	Accuracy	Old/New
Reward	986 (57)	51 (1.0)	87 (3.0)
Zero	985 (57)	51 (0.8)	80 (3.7)
Loss	978 (56)	52 (0.8)	83 (3.7)
Happy	1011 (58)	53 (0.9)	86 (3.2)
Neutral	1006 (55)	51 (0.9)	78 (4.0)
Angry	1014 (58)	51 (1.0)	89 (3.4)

Table 4

Repeated-measures ANOVA results for all ERP and pupil size data (time windows are referring to target face onset) of the test session, including F-, p- and η^2_p -values. Only significant post-hoc pairwise comparisons (after Bonferroni correction) are reported.

Test Session				
Associated Motivational Salience				
	Main Effect Motivation	Gain—Zero Outcome	Loss—Zero Outcome	Gain—Loss
P1 target (75–125 ms)	$F(2,86) = 0.893$ $p = 0.413$ $\eta^2_p = 0.020$			
N170 target (130–180 ms)	$F(2,86) = 1.241$ $p = 0.293$ $\eta^2_p = 0.028$			
EPN target (200–350 ms)	$F(2,86) = 1.547$ $p = 0.219$ $\eta^2_p = 0.035$			
P3 target (200–350 ms)	$F(2,86) = 5.124$ $p = 0.008$ $\eta^2_p = 0.106$	$F(1,43) = 8.346$ $p = 0.018$ $\eta^2_p = 0.163$		
LPC target (350–700 ms)	$F(2,86) = 10.632$ $p < 0.001$ $\eta^2_p = 0.198$	$F(1,43) = 18.792$ $p < 0.001$ $\eta^2_p = 0.304$		$F(1,43) = 8.880$ $p = 0.015$ $\eta^2_p = 0.171$
Pupil size (1090–3590 ms)	$F(2,58) = 0.049$ $p = 0.950$ $\eta^2_p = 0.002$			
Inherent Emotional Salience				
	Main Effect Emotion	Happy- Neutral	Angry- Neutral	Angry- Happy
P1 target (75–125 ms)	$F(2,86) = 1.790$ $p = 0.173$ $\eta^2_p = 0.040$			
N170 target (130–180 ms)	$F(2,86) = 7.901$ $p = 0.001$ $\eta^2_p = 0.155$		$F(1,43) = 13.695$ $p = 0.003$ $\eta^2_p = 0.242$	$F(1,43) = 8.941$ $p = 0.015$ $\eta^2_p = 0.172$
EPN target (200–350 ms)	$F(2,86) = 21.217$ $p < 0.001$ $\eta^2_p = 0.330$	$F(1,43) = 34.587$ $p < 0.001$ $\eta^2_p = 0.446$	$F(1,43) = 39.982$ $p < 0.001$ $\eta^2_p = 0.482$	
LPC target (350–700 ms)	$F(2,86) = 1.266$ $p = 0.287$ $\eta^2_p = 0.029$			
Pupil size (1090–3590 ms)	$F(2,58) = 0.705$ $p = 0.498$ $\eta^2_p = 0.024$			

emotion-related EPN distribution, topography comparisons were computed between the typical EPN distributions elicited by facial expressions of emotion and the cue-elicited ERP activity 200–300 ms after cue onset. Specifically, the difference topography of gain minus zero-outcome cues in the learning session was compared with the difference topography of happy minus neutral expressions in the test session. The topography \times electrode interaction revealed no significant difference between these two topographies, $F(63,2709) = 0.840$, $p = 0.594$, $\eta^2_p = 0.019$. Similarly, the difference topography of loss minus zero-outcome cues was compared to the difference topography of angry minus neutral expressions of the test session. Again, the topography \times electrode interaction failed significance between these two topographies, $F(63,2709) = 1.325$, $p = 0.146$, $\eta^2_p = 0.030$.

Please note that we report findings from additional analyses (accuracy per target face in the learning session, the prediction of test phase data by learning phase physiological indicators, additional analyses on ERPs after applying a baseline prior to the target faces, and analyses of the ERP data of the test phase in a full 3×2 factorial design) in the Supplementary Materials.

Discussion

The main aim of the present study was to investigate whether implicitly learned associations of motivational salience result in a prioritized processing, similar to previously shown explicit associations or inherent emotional salience (e.g., Hammerschmidt et al., 2017). To this end, we implemented a multi-measure approach, considering ERPs

as indicator of neural processing, pupil dilations as a correlate of arousal, and behavioral parameters as control variables. During a learning session, a sequential face-matching task was combined with different motivational contexts that were indicated by preceding cues and feedback about monetary outcome at the end of each trial. To address our second aim, the amount of monetary gain and loss was equalized in order to compare their impact on the neural processing. On the following day, the previously associated faces were presented together with novel faces with expressions of emotion (happiness, anger) and neutrality, allowing for a direct comparison of potential effects driven by associated versus inherent salience during face processing.

Implicitly acquired reward associations improve stimulus processing

Our main finding is a long-lasting ERP effect of gain implicitly associated to the target faces that became evident from 200 to 700 ms after stimulus onset in the test session. Across the whole time window, highly similar ERP modulations (confirmed by topography comparison) occurred that consisted of increased centro-parietal positivities. These ERP modulations presumably resemble subsequent P3 and LPC components - linked to an early onset of higher-order stimulus evaluations - that were particularly boosted for gain-associated faces. Such modulations of late processing stages (P3/LPC) by monetary reward have been previously demonstrated in studies employing associative learning based on explicit valence categorization (Schacht et al., 2012; Rossi et al., 2017). These previous findings have been interpreted to indicate that previously rewarded stimuli receive increased cognitive resources, resulting in a

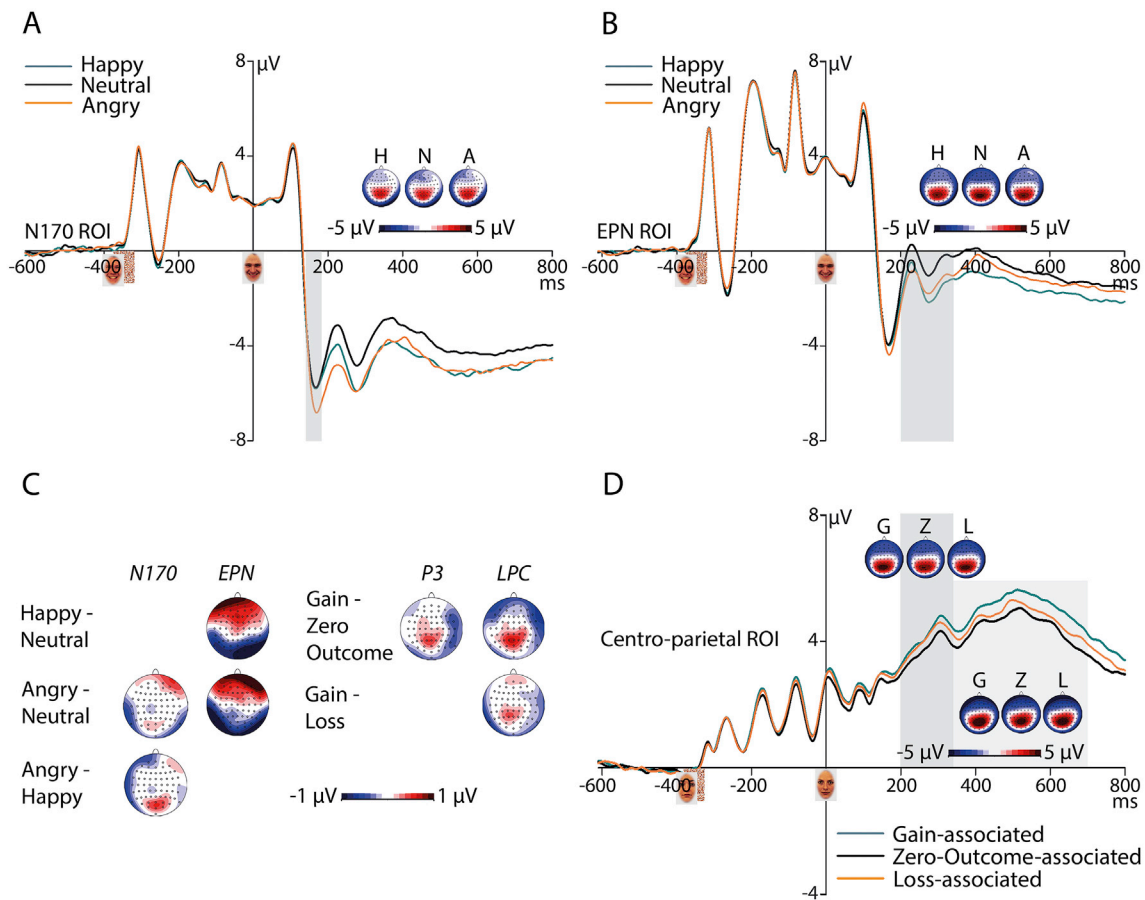


Fig. 4. Grand average ERPs within the N170 ROI (panel A), the EPN ROI (panel B) and the centro-parietal/LPC ROI (panel D). Corresponding ERP topographies for each motivation/emotion conditions are depicted in the embedded heads. ERP differences between indicated emotion/motivation categories are shown in panel C, for inherent emotional faces (left) and faces previously associated with monetary outcome (right). Highlighted areas display the time windows of analyses.

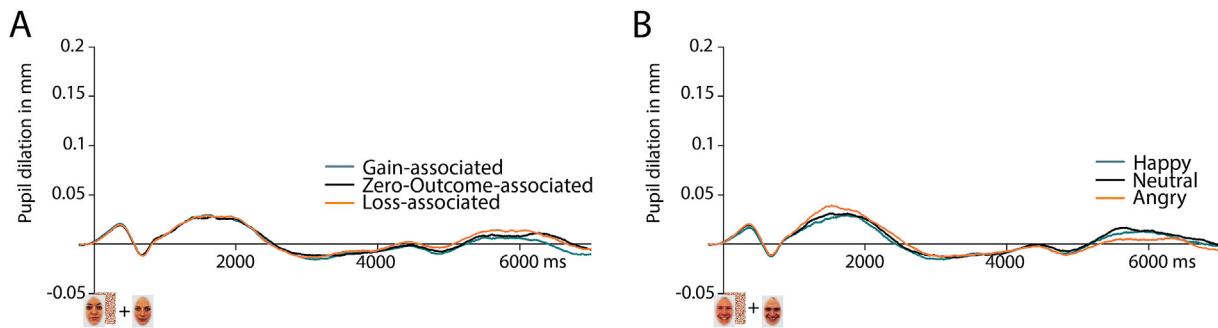


Fig. 5. Pupil dilations during the test session for (A) previously associated and (B) inherent emotional and neutral expressions.

prioritized processing (Nieuwenhuis et al., 2005), even for implicit reward associations (Bourgeois et al., 2016). In particular, the P3/LPC modulations on previously associated faces deserve special attention for three reasons: First, we did not find significant modulations of ERPs by motivational incentives after target face onset during the learning session. Second, the condition-to-face assignments were not made explicit for the participants during the learning session. Third, the modulation of the LPC component by gain association remained even if those trials were excluded that consisted of target faces correctly assigned to the outcome condition in the manipulation check after the learning session. This finding strongly indicates that this effect was driven by implicit associations of the motivational contexts to certain faces. One potential explanation of these findings relates to the time required for consolidation that has been proposed in particular for arousing stimuli (Sharot

et al., 2004). Therefore, overnight consolidation might play a crucial role particularly during the implicit association of motivational salience as similar P3 effects modulated by monetary reward were observed during an explicit learning paradigm without delay between learning and testing (Rossi et al., 2017).

In contrast to previous associative learning studies, in particular to Hammerschmidt and colleagues (Hammerschmidt et al., 2017) who detected P1 modulations driven by monetary reward associations, no ERP modulations at short latencies were found in the present study. Two reasons for this finding are conceivable: First, as early ERP effects of acquired salience were detected in studies employing explicit associative learning, implicitly learned associations might lead to less apparent impacts on perceptual encoding of the certain stimuli. Second, the task demands in the present study were exceptionally high and might have

suppressed early ERP modulations (e.g., Pessoa, 2014). In order to check whether the present study design actually allows for typical emotion-related ERP modulations and to compare the effects elicited by associated motivational salience to effects of inherent emotional salience (cf., Hammerschmidt et al., 2017), novel identities with facial expressions of emotion were presented in the same task during the test session. Modulations of two emotion-related ERP components occurred: The face-sensitive N170 component was modulated by angry facial expressions compared to both neutral and happy expressions, supporting our previous findings (Hammerschmidt et al., 2017) that the N170 is, amongst others, influenced by negative expressions (for reviews, see Rellecke et al., 2013; Hinojosa et al., 2015). However, the impact of the potentially differing intensity of the emotional expressions (the angry expressions might be perceived as more intense than the happy expressions) needs to be taken into account (cf., Hinojosa et al., 2015). It was further suggested that the N170 might be overlapped by the directly following EPN component which leads to comparable modulations by emotional expressions (Schacht and Sommer, 2009; Rellecke et al., 2011, 2012). For the EPN component, typical modulations were found for happy and angry compared to neutral facial expressions (e.g., Hammerschmidt et al., 2017), as the EPN is known to reflect the automatic encoding of the emotional content of a given stimulus independent of task demands (Rellecke et al., 2011). In addition to N170 and EPN, previous studies reported even earlier (P1) or later LPC modulations (e.g., Schupp et al., 2004; Rellecke et al., 2012; Hammerschmidt et al., 2017), but in the present study those modulations were absent, potentially due to the task-irrelevance of the expressed emotion. Further, also repetition effects are conceivable due to the high number of trials showing the same target face identity during learning (40 repetitions) and testing (also 40 repetitions) (for a review, see Ferrari et al., 2017). Therefore, the present study design indeed allows for typical emotion-related ERP modulations; however, P1 modulations, known to be task-dependent (Pratt et al., 2011; Rellecke et al., 2012), might be suppressed by the high cognitive load of the task used in the present study. Despite the differences in results between our previous (Hammerschmidt et al., 2017) and the current study, the latter provides additional evidence for substantial differences in the processing of inherent emotional and associated motivational salience. Together, this argues against a common mechanism of these two sources of salience on stimulus processing. In addition, future research is needed to investigate not only whether happy and especially angry facial expressions are a suitable equivalent for monetary reward and loss, as a debate is ongoing whether they elicit approach and/or avoidance behavior (e.g., Paulus and Wentura, 2014, 2016), but also whether the present effects might additionally be elicited by faces expressing fear or sadness.

Motivational contexts boost subsequent processing of even task-irrelevant stimuli

Recent studies provided robust evidence for impacts of motivational context on target stimulus processing (e.g., Krebs and Woldorff, 2017), interestingly taking place even before effects of spatial attention occur (Bayer et al., 2017). What has yet been largely neglected is the question whether the motivational salience of cue stimuli might lead to preferential processing similar to stimuli of varying emotional content, such as affective scenes or emotional expressions (cf., Anderson, 2013). Using cue stimuli of identical shape that only differed in color (counter-balanced), allowed us to investigate potential ERP modulations through the cues' meaning, by keeping visual features constant across conditions. Interestingly, we found increased ERP effects to gain- and loss-indicating cues that resembled typical ERP modulations driven by stimuli of emotional content across different domains, i.e. EPN and LPC effects (e.g., Schacht and Sommer, 2009; Bayer and Schacht, 2014). This impression was verified by topography comparisons between these ERP responses to the cues during the learning session and to EPN effects elicited by emotional expressions during the test session in the present

study. The first visually evoked ERP component after cue onset – the P1 – did not differ as a function of the cues' motivational salience. As cue stimuli in the present study were perceptually identical besides variation in three equi-luminant colors, the lack of P1 effects eventually indicates that previously reported P1 effects modulated by emotional valence (e.g., Pourtois et al., 2004; Rellecke et al., 2012) might reflect rapid core-feature analysis under the precondition that these features are clearly discriminable (Fedota et al., 2012).

Impacts of motivational context were, importantly, not restricted to the processing of cues but extended to the subsequent processing of even task-irrelevant stimuli within trials of increased motivational salience during the learning session. These impacts, however, declined when the target face was presented. As studies using associative learning paradigms typically report stabilized associated effects on target processing (e.g., Schacht et al., 2012; Wieser et al., 2014; Hammerschmidt et al., 2017; Kulke et al., 2017), future research is needed to determine the emergence of those associated effects.

Effects on pupil dilations

In the learning session, pupil dilations were enlarged for both gain- and loss-related contexts compared to zero-outcome-related contexts. These findings indicate increased arousal or attention triggered by motivational incentives (Massar et al., 2016; Pulcu and Browning, 2017). In the test session, although LPC modulations driven by reward associations were detected on the neural level, pupil size did not differ as a function of associated motivational salience, indicating that physiological arousal only increases when motivational incentives are directly available. Furthermore, pupil size was also not impacted by facial expressions carrying inherent emotional salience (although they elicited EPN modulations on the neural level), contradicting previous findings (Kret et al., 2013), indicating that impacts of emotional expressions might be suppressed by the cognitive load of the task and the consequential task-irrelevance of the expressed emotion.

Impacts of monetary gain and loss under conditions of equalized outcomes

In contrast to recent studies, which typically linked incentives explicitly to successful learning, the present study design ensured equalized outcomes of monetary gain and loss, but nevertheless demonstrated a prioritized neural processing of gain over loss. The influential prospect theory in economic decision making (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992) already suggested an asymmetric function of gains and losses – with a typically higher impact of losses than gains during risky choices. This asymmetry is potentially based on the activation of different brain areas (Trepel et al., 2005), especially during reinforcement learning tasks (Wächter et al., 2009; Kim et al., 2015). In contrast, visual selective attention studies revealed an advantage of gains over losses in the prioritized processing (for a review, see Chelazzi et al., 2013; Barbaro et al., 2017). Recently, a first explanation for these seemingly conflicting assumptions was proposed based on findings that gain-associated targets were processed faster than loss-associated targets (Chapman et al., 2015). The authors concluded that the inhibition necessary for loss aversion takes more time than the facilitated processing elicited by reward associations.

Conclusion

The present findings demonstrate that motivational contexts impacted pupil dilation and led to an ongoing influence on the neural processing of subsequent visual stimuli (fixation cross, prime/mask) during the learning session, however, not persisting to the target faces. During the test session, implicitly associated motivational salience impacted the processing of inherently neutral faces, reflected in an enhanced centro-parietal ERP modulation for previously gain-associated target faces linked to higher-order processing stages. In contrast, target

faces expressing emotions (happy, angry) modulated the typical emotion-related EPN component, whereas P1 and LPC modulations were suppressed presumably by high demanding task requirements. In summary, this study provides new evidence that neural representations of neutral stimuli can acquire increased salience via implicit learning reflected in a preferential processing on cognitive evaluation stages. In contrast, facial expressions of emotion modulated the N170 and the EPN component indicating a dissociation of the processing of inherent emotional and associated motivational salience. In addition, an advantage for gain over loss associations is unveiled, even when their occurrence is equalized, indicating distinct differences in their neural processing.

Funding

This work was funded by the German Research Foundation (grant #SCHA1848/1-1 to AS) and by the Leibniz ScienceCampus Primate Cognition (grants to AS and IK).

Acknowledgments

The authors thank Anna-Maria Grimm and Rebecca Jacob for their contributions to the development of the study design and data collection, Florian Niefind and Kay Reimers for their technical support during experimental setup, and Benthe Kornrumpf and Anton Unakafov for providing codes for data analyses.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2018.06.055>.

References

- Abdel Rahman, R., Sommer, W., 2012. Knowledge scale effects in face recognition: an electrophysiological investigation. *Cognit. Affect. Behav. Neurosci.* 12, 161–174. <https://doi.org/10.3758/s13415-011-0063-9>.
- Anderson, A.K., 2005. Affective influences on the attentional dynamics supporting awareness. *J. Exp. Psychol. Gen.* 134, 258–281. <https://doi.org/10.1037/0096-3445.134.2.258>.
- Anderson, B.A., 2013. A value-driven mechanism of attentional selection. *J. Vis.* 13, 1–16. <https://doi.org/10.1167/13.3.7>.
- Barbaro, L., Peelen, M.V., Hickey, C., 2017. Valence, not utility, underlies reward-driven prioritization in human vision. *J. Neurosci.* <https://doi.org/10.1523/JNEUROSCI.1128-17.2017>, 1128–117.
- Batterink, L., Neville, H., 2011. Implicit and explicit mechanisms of word learning in a narrative context: an event-related potential study. *J. Cognit. Neurosci.* 23, 3181–3196. <https://doi.org/10.1162/jocn>.
- Batty, M., Taylor, M.J., 2003. Early processing of the six basic facial emotional expressions. *Cognit. Brain Res.* 17, 613–620. [https://doi.org/10.1016/S0926-6410\(03\)00174-5](https://doi.org/10.1016/S0926-6410(03)00174-5).
- Bayer, M., Rossi, V., Vanlessen, N., Grass, A., Schacht, A., Pourtois, G., 2017. Independent effects of motivation and spatial attention in the human visual cortex. *Soc. Cogn. Affect. Neuroscience* 12, 146–156. <https://doi.org/10.1093/scan/nsw162>.
- Bayer, M., Schacht, A., 2014. Event-related brain responses to emotional words, pictures, and faces - a cross-domain comparison. *Front. Psychol.* 5, 1–10. <https://doi.org/10.3389/fpsyg.2014.01106>.
- Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. *J. Cognit. Neurosci.* 8, 551–565.
- Berridge, C.W., Waterhouse, B.D., 2003. The locus coeruleus-noradrenergic system: modulation of behavioral state and state-dependent cognitive processes. *Brain Res. Rev.* E, 42, 33–84. [https://doi.org/10.1016/S0165-0173\(03\)00143-7](https://doi.org/10.1016/S0165-0173(03)00143-7).
- Berry, D.C., Dienes, Z., 1993. *Implicit Learning: Theoretical and Empirical Issues*. Erlbaum, Hove, U.K.
- Bourgeois, A., Neveu, R., Vuilleumier, P., 2016. How does awareness modulate goal-directed and stimulus-driven shifts of attention triggered by value learning? *PLoS One* 11. <https://doi.org/10.1371/journal.pone.0160469> e0160469.
- Bradley, M.M., Miccoli, L., Escrig, M.A., Lang, P.J., 2008. The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology* 45, 602–607. <https://doi.org/10.1111/j.1469-8986.2008.00654.x>.
- Brunyé, T.T., Gardony, A.L., 2017. Eye tracking measures of uncertainty during perceptual decision making. *Int. J. Psychophysiol.* 120, 60–68. <https://doi.org/10.1016/j.ijpsycho.2017.07.008>.
- Calvo, M.G., Lundqvist, D., 2008. Facial expressions of emotion (KDEF): identification under different display-duration conditions. *Behav. Res. Meth.* 40, 109–115. <https://doi.org/10.3758/BRM.40.1.109>.
- Chapman, C.S., Gallivan, J.P., Wong, J.D., Wispinski, N.J., Enns, J.T., 2015. The snooze of lose: rapid reaching reveals that losses are processed more slowly than gains. *J. Exp. Psychol. Gen.* 144, 844–863. <https://doi.org/10.1037/xge0000085>.
- Chelazzi, L., Perlati, A., Santandrea, E., Della Libera, C., 2013. Rewards teach visual selective attention. *Vis. Res.* 85, 58–62. <https://doi.org/10.1016/j.visres.2012.12.005>.
- Cleeremans, A., Destrebecqz, A., Boyer, M., 1998. Implicit learning: news from the front. *Trends Cognit. Sci.* 2, 406–416. [https://doi.org/10.1016/S1364-6613\(98\)01232-7](https://doi.org/10.1016/S1364-6613(98)01232-7).
- Connor, C.E., Egeth, H.E., Yantis, S., 2004. Visual attention: bottom-up versus top-down. *Curr. Biol.* 14, 850–852. <https://doi.org/10.1016/j.cub.2004.09.041>.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215. <https://doi.org/10.1038/nrn755>.
- Cuthbert, B.N., Schupp, H.T., Bradley, M.M., Birbaumer, N., Lang, P.J., 2000. Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biol. Psychol.* 52, 95–111. [https://doi.org/10.1016/S0301-0511\(99\)00044-7](https://doi.org/10.1016/S0301-0511(99)00044-7).
- Della Libera, C., Chelazzi, L., 2006. Visual selective attention and the effects of monetary rewards. *Psychol. Sci.* 17, 222–227. <https://doi.org/10.1111/j.1467-9280.2006.01689.x>.
- Di Russo, F., Martinez, A., Hillyard, S.A., 2003. Source analysis of event-related cortical activity during visuo-spatial attention. *Cerebr. Cortex* 13, 486–499. <https://doi.org/10.1093/cercor/13.5.486>.
- Eastwood, J.D., Smilek, D., Merikle, P.M., 2001. Differential attentional guidance by unattended faces expressing positive and negative emotion. *Percept. Psychophys.* 63, 1004–1013. <https://doi.org/10.3758/BF03194519>.
- Einhäuser, W., Stout, J., Koch, C., Carter, O., 2008. Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proc. Natl. Acad. Sci. Unit. States Am.* 105, 1704–1709. <https://doi.org/10.1073/pnas.0707727105>.
- Failing, M., Theeuwes, J., 2017. Selection history: how reward modulates selectivity of visual attention. *Psychon. Bull. Rev.* 1–25. <https://doi.org/10.3758/s13423-017-1380-y>.
- Fedota, J.R., McDonald, C.G., Roberts, D.M., Parasuraman, R., 2012. Contextual task difficulty modulates stimulus discrimination: electrophysiological evidence for interaction between sensory and executive processes. *Psychophysiology* 49, 1384–1393. <https://doi.org/10.1111/j.1469-8986.2012.01455.x>.Contextual.
- Ferrari, V., Codispoti, M., Bradley, M.M., 2017. Repetition and ERPs during emotional scene processing: a selective review. *Int. J. Psychophysiol.* 111, 170–177. <https://doi.org/10.1016/j.ijpsycho.2016.07.496>.
- Frith, C., 2009. Role of facial expressions in social interactions. *Philos. Trans. R. Soc. B Biol. Sci.* 364, 3453–3458. <https://doi.org/10.1098/rstb.2009.0142>.
- Gilzenrat, M.S., Nieuwenhuis, S., Jepma, M., Cohen, J.D., 2010. Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function. *Cognit. Affect. Behav. Neurosci.* 10, 252–269. <https://doi.org/10.3758/CABN.10.2.252>.
- Grandjean, D., Sander, D., Scherer, K.R., 2008. Conscious emotional experience emerges as a function of multilevel, appraisal-driven response synchronization. *Conscious. Cognit.* 17, 484–495. <https://doi.org/10.1016/j.concog.2008.03.019>.
- Hammerschmidt, W., Sennhenn-Reulen, H., Schacht, A., 2017. Associated motivational salience impacts early sensory processing of human faces. *Neuroimage* 156, 466–474. <https://doi.org/10.1016/j.neuroimage.2017.04.032>.
- Hinojosa, J.A., Mercado, F., Carretié, L., 2015. N170 sensitivity to facial expression: a meta-analysis. *Neurosci. Biobehav. Rev.* 55, 498–509. <https://doi.org/10.1016/j.neubiorev.2015.06.002>.
- Hintze, P., Junghöfer, M., Bruchmann, M., 2014. Evidence for rapid prefrontal emotional evaluation from visual evoked responses to conditioned gratings. *Biol. Psychol.* 99, 125–136. <https://doi.org/10.1016/j.biopsycho.2014.03.010>.
- Ille, N., Berg, P., Scherg, M., 2002. Artifact correction of the ongoing EEG using spatial filters based on artifact and brain signal topographies. *J. Clin. Neurophysiol.* 19, 113–124. <https://doi.org/10.1097/00004691-200203000-00002>.
- Junghöfer, M., Bradley, M.M., Elbert, T.R., Lang, P.J., 2001. Fleeting images: a new look at early emotion discrimination. *Psychophysiology* 38, 175–178. <https://doi.org/10.1017/S0048577201000762>.
- Kahneman, D., 1973. *Attention and Effort*. Prentice-Hall, Englewood Cliffs.
- Kahneman, D., Tversky, A., 1979. Prospect Theory: an analysis of decision under risk. *Econometrica* 47, 263–291. <https://doi.org/10.1111/j.1536-7150.2011.00774.x>.
- Kang, O.E., Huffer, K.E., Wheatley, T.P., 2014. Pupil dilation dynamics track attention to high-level information. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0102463>.
- Kim, S.H., Yoon, H.S., Kim, H., Hamann, S., 2015. Individual differences in sensitivity to reward and punishment and neural activity during reward and avoidance learning. *Soc. Cogn. Affect. Neuroscience* 10, 1219–1227. <https://doi.org/10.1093/scan/nsv007>.
- Klein, F., Iffland, B., Schindler, S., Wabnitz, P., Neuner, F., 2015. This person is saying bad things about you: the influence of physically and socially threatening context information on the processing of inherently neutral faces. *Cogn. Affect. Behav. Neuroscience* 15, 736–748. <https://doi.org/10.3758/s13415-015-0361-8>.
- Krebs, R.M., Boehler, C.N., Woldorff, M.G., 2010. The influence of reward associations on conflict processing in the Stroop task. *Cognition* 117, 341–347. <https://doi.org/10.1016/j.cognition.2010.08.018>.
- Krebs, R.M., Woldorff, M.G., 2017. Cognitive control and reward. In: Egner, T. (Ed.), *The Wiley Handbook of Cognitive Control*, first ed. Wiley-Blackwell: John Wiley and Sons, Ltd., pp. 422–439.
- Kret, M.E., Roelofs, K., Stekelenburg, J.J., de Gelder, B., 2013. Emotional signals from faces, bodies and scenes influence observers' face expressions, fixations and pupil-size. *Front. Hum. Neurosci.* 7, 1–9. <https://doi.org/10.3389/fnhum.2013.00810>.

- Krishnamoorthy, K., Thomson, J., Cai, Y., 2004. An exact method of testing equality of several binomial proportions to a specified standard. *Comput. Stat. Data Anal.* 45, 697–707. [https://doi.org/10.1016/S0167-9473\(03\)00095-1](https://doi.org/10.1016/S0167-9473(03)00095-1).
- Kulke, L., Bayer, M., Grimm, A.M., Schacht, A., 2017. Differential effects of learned associations with words and pseudowords on event-related brain potentials. *bioRxiv*. <https://doi.org/10.1101/240945>.
- Laeng, B., Sirois, S., Gredebäck, G., 2012. Pupillometry. *Perspect. Psychol. Sci.* 7, 18–27. <https://doi.org/10.1177/1745691611427305>.
- Lang, P.J., Bradley, M.M., 2010. Emotion and the motivational brain. *Biol. Psychol.* 84, 437–450. <https://doi.org/10.1016/j.biopsycho.2009.10.007>.
- Langton, S.R.H., Law, A.S., Burton, A.M., Schweinberger, S.R., 2008. Attention capture by faces. *Cognition* 107, 330–342. <https://doi.org/10.1016/j.cognition.2007.07.012>.
- Lundqvist, D., Flykt, A., Öhman, A., 1998. The Karolinska Directed Emotional Faces -KDEF, CD ROM from Department of Clinical Neuroscience. Psychology section, Karolinska Institutet. ISBN 91-630-7164-9.
- Massar, S.A.A., Lim, J., Sasmita, K., Chee, M.W.L., 2016. Rewards boost sustained attention through higher effort: a value-based decision making approach. *Biol. Psychol.* 120, 21–27. <https://doi.org/10.1016/j.biopsycho.2016.07.019>.
- Mathôt, S., Siebold, A., Donk, M., Vitu, F., 2015. Large pupils predict goal-driven eye movements. *J. Exp. Psychol. Gen.* 144, 513–521. <https://doi.org/10.1037/a0039168>.
- Meadows, C.C., Gable, P.A., Lohse, K.R., Miller, M.W., 2016. The effects of reward magnitude on reward processing: an averaged and single trial event-related potential study. *Biol. Psychol.* 118, 154–160. <https://doi.org/10.1016/j.biopsycho.2016.06.002>.
- Murphy, P.R., O'Connell, R.G., O'Sullivan, M., Robertson, I.H., Balsters, J.H., 2014. Pupil diameter covaries with BOLD activity in human locus coeruleus. *Hum. Brain Mapp.* 35, 4140–4154. <https://doi.org/10.1002/hbm.22466>.
- Nieuwenhuis, S., Aston-Jones, G., Cohen, J.D., 2005. Decision making, the P3, and the locus coeruleus-norepinephrine system. *Psychol. Bull.* 131, 510–532. <https://doi.org/10.1037/0033-2909.131.4.510>.
- Öhman, A., Mineka, S., 2001. Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* 108, 483–522.
- Oldfield RC, 1971. The assessment and analysis of Handedness: the edinburgh inventory. *Neuropsychologia* 9, 97–113. [https://doi.org/10.1016/0028-3932\(71\)90067-4](https://doi.org/10.1016/0028-3932(71)90067-4).
- Olofsson, J.K., Nordin, S., Sequeira, H., Polich, J., 2008. Affective picture processing: an integrative review of ERP findings. *Biol. Psychol.* 77, 247–265. <https://doi.org/10.1016/j.biopsycho.2007.11.006>.
- Partala, T., Surakka, V., 2003. Pupil size variation as an indication of affective processing. *Int. J. Hum. Comput. Stud.* 59, 185–198. [https://doi.org/10.1016/S1071-5819\(03\)00017-X](https://doi.org/10.1016/S1071-5819(03)00017-X).
- Paulus, A., Wentura, D., 2014. Threatening joy: approach and avoidance reactions to emotions are influenced by the group membership of the expresser. *Cognit. Emot.* 28 (4), 656–677. <https://doi.org/10.1080/02699931.2013.849659>.
- Paulus, A., Wentura, D., 2016. It depends: approach and avoidance reactions to emotional expressions are influenced by the contrast emotions presented in the task. *J. Exp. Psychol. Hum. Percept. Perform.* 42 (2), 197–212. <https://doi.org/10.1037/xhp0000130>.
- Pessoa, L., 2014. Multiple influences of reward on perception and attention. *Vis. cogn.* 23, 272–290. <https://doi.org/10.1080/13506285.2014.974729>.
- Peysakhovich, V., Causse, M., Scannella, S., Dehaes, F., 2015. Frequency analysis of a task-evoked pupillary response: luminance-independent measure of mental effort. *Int. J. Psychophysiol.* 97, 30–37. <https://doi.org/10.1016/j.ijpsycho.2015.04.019>.
- Pivik, R.T., Broughton, R.J., Coppola, R., Davidson, R.J., Fox, N.A., Nuwer, M.R., 1993. Guidelines for the recording and quantitative analysis of electroencephalographic activity in research contexts. *Psychophysiology* 30, 547–558.
- Pourtois, G., Grandjean, D., Sander, D., Vuilleumier, P., 2004. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cerebr. Cortex* 14, 619–633. <https://doi.org/10.1093/cercor/bhh023>.
- Pratt, N., Willoughby, A., Swick, D., 2011. Effects of working memory load on visual selective attention: behavioral and electrophysiological evidence. *Front. Hum. Neurosci.* 5, 1–9. <https://doi.org/10.3389/fnhum.2011.00057>.
- Pulcu, E., Browning, M., 2017. Affective bias as a rational response to the statistics of rewards and punishments. *Elife* 6. <https://doi.org/10.7554/eLife.27879> e27879.
- Rellecke, J., Palazova, M., Sommer, W., Schacht, A., 2011. On the automaticity of emotion processing in words and faces: event-related brain potentials evidence from a superficial task. *Brain Cognit.* 77, 23–32. <https://doi.org/10.1016/j.bandc.2011.07.001>.
- Rellecke, J., Sommer, W., Schacht, A., 2012. Does processing of emotional facial expressions depend on intention? Time-resolved evidence from event-related brain potentials. *Biol. Psychol.* 90, 23–32. <https://doi.org/10.1016/j.biopsycho.2012.02.002>.
- Rellecke, J., Sommer, W., Schacht, A., 2013. Emotion effects on the N170: a question of reference? *Brain Topogr.* 26, 62–71. <https://doi.org/10.1007/s10548-012-0261-y>.
- Rossi, V., Vanlessen, N., Bayer, M., Grass, A., Pourtois, G., Schacht, A., 2017. Motivational salience modulates early visual cortex responses across task sets. *J. Cognit. Neurosci.* 29, 968–979. <https://doi.org/10.1162/jocn>.
- Satterthwaite, T.D., Green, L., Myerson, J., Parker, J., Ramaratnam, M., Buckner, R.L., 2007. Dissociable but inter-related systems of cognitive control and reward during decision making: evidence from pupillometry and event-related fMRI. *Neuroimage* 37, 1017–1031. <https://doi.org/10.1016/j.neuroimage.2007.04.066>.
- Schacht, A., Adler, N., Chen, P., Guo, T., Sommer, W., 2012. Association with positive outcome induces early effects in event-related brain potentials. *Biol. Psychol.* 89, 130–136. <https://doi.org/10.1016/j.biopsycho.2011.10.001>.
- Schacht, A., Sommer, W., 2009. Emotions in word and face processing: early and late cortical responses. *Brain Cognit.* 69, 538–550. <https://doi.org/10.1016/j.bandc.2008.11.005>.
- Scherer, K.R., 2005. What are emotions? And how can they be measured? *Soc. Sci. Inf.* 44, 695–729. <https://doi.org/10.1177/0539018405058216>.
- Scherer, K.R., 2009. The dynamic architecture of emotion: evidence for the component process model. *Cogn. Emotion* 23, 1307–1351. <https://doi.org/10.1080/02699930902928969>.
- Scherg, M., 2003. Artifacts: Using Calibration Data to Generate Artifact Coefficients (Version 5.0). Manual for BESA: Brain-electrical Source Analysis Software. Megis Software GmbH, Munich, Germany.
- Scheuthle, H., Carabias-Hütter, V., Kaiser, F.G., 2005. The motivational and instantaneous behavior effects of contexts: steps toward a theory of goal-directed behavior. *J. Appl. Soc. Psychol.* 35, 2076–2093. <https://doi.org/10.1111/j.1559-1816.2005.tb02210.x>.
- Schupp, H.T., Öhman, A., Junghöfer, M., Weike, A.I., Stockburger, J., Hamm, A.O., 2004. The facilitated processing of threatening faces: an ERP analysis. *Emotion* 4, 189–200. <https://doi.org/10.1037/1528-3542.4.2.189>.
- Sharot, T., Delgado, M.R., Phelps, E.A., 2004. How emotion enhances the feeling of remembering. *Nat. Neurosci.* 7, 1376–1380. <https://doi.org/10.1038/nn1353>.
- Skrandies, W., 1990. Global field power and topographic similarity. *Brain Topogr.* 3, 137–141. <https://doi.org/10.1007/BF01128870>.
- Smallwood, J., Brown, K.S., Tipper, C., Giesbrecht, B., Franklin, M.S., Mrazek, M.D., Carlson, J.M., Schooler, J.W., 2011. Pupillometric evidence for the decoupling of attention from perceptual input during offline thought. *PLoS One* 6. <https://doi.org/10.1371/journal.pone.0018298>.
- Stolarova, M., Keil, A., Moratti, S., 2006. Modulation of the C1 visual event-related component by conditioned stimuli: evidence for sensory plasticity in early affective perception. *Cerebr. Cortex* 16, 876–887. <https://doi.org/10.1093/cercor/bhj031>.
- Suess, F., Rabovsky, M., Rahman, R.A., 2013. Perceiving emotions in neutral faces: expression processing is biased by affective person knowledge. *Soc. Cogn. Affect. Neurosci.* 10, 531–536. <https://doi.org/10.1093/scan/nsu088>.
- Trepel, C., Fox, C.R., Poldrack, R.A., 2005. Prospect theory on the brain? Toward a cognitive neuroscience of decision under risk. *Cognit. Brain Res.* 23, 34–50. <https://doi.org/10.1016/j.cogbrainres.2005.01.016>.
- Tversky, A., Kahneman, D., 1992. Advances in prospect theory - cumulative representation of uncertainty. *J. Risk Uncertain* 5, 297–323. <https://doi.org/10.1007/BF00122574>.
- Unakafov, A.M., 2017. An exact test for equality of several binomial proportions to a specified standard. MATLAB Central File Exchange. retrieved Nov 08, 2017. <https://de.mathworks.com/matlabcentral/fileexchange/64987-an-exact-test-for-equality-of-several-binomial-proportions-to-a-specified-standard>.
- Urai, A.E., Braun, A., Donner, T.H., 2017. Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias. *Nat. Commun.* 8, 14637. <https://doi.org/10.1038/ncomms14637>.
- Vuilleumier, P., 2005. How brains beware: neural mechanisms of emotional attention. *Trends Cognit. Sci.* 9, 585–594. <https://doi.org/10.1016/j.tics.2005.10.011>.
- Wächter, T., Lungu, O., Liu, T., Willingham, D.T., Ashe, J., 2009. Differential effect of reward and punishment on preceudural learning. *Brain Behav. Immunity* 29, 436–443. <https://doi.org/10.1523/JNEUROSCI.4132-08.2009>.Differential.
- Wei, P., Wang, D., Ji, L., 2016. Reward expectation regulates brain responses to task-relevant and task-irrelevant emotional words: ERP evidence. *Soc. Cogn. Affect. Neurosci.* 11, 191–203. <https://doi.org/10.1093/scan/nsv097>.
- Wieser, M.J., Gerdes, A.B.M., Büngel, I., Schwarz, K.A., Mühlberger, A., Pauli, P., 2014. Not so harmless anymore: how context impacts the perception and electrocortical processing of neutral faces. *Neuroimage* 92, 74–82. <https://doi.org/10.1016/j.neuroimage.2014.01.022>.
- Xu, M., Li, Z., Diao, L., Fan, L., Yang, D., 2016. Contextual valence and sociality jointly influence the early and later stages of neutral face processing. *Front. Psychol.* 7, 1–10. <https://doi.org/10.3389/fpsyg.2016.01258>.
- Zeelenberg, R., Wagenmakers, E.-J., Rotteveel, M., 2006. The impact of emotion on perception: bias or enhanced processing? *Psychol. Sci.* 17, 287–291. <https://doi.org/10.1111/j.1467-9280.2006.01700.x>.
- Zheng, Y., Li, Q., Zhang, Y., Li, Q., Shen, H., Gao, Q., Zhou, S., 2017. Reward processing in gain versus loss context: an ERP study. *Psychophysiology* 54, 1040–1053. <https://doi.org/10.1111/psyp.12855>.